Matrix Population Models for Wildlife Conservation and Management

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Lecture 4
Generation time

Alfred J. LOTKA,
The father of « mathematical demography »

Like most mathematicians, he takes the hopeful biologist to the edge of a pond, points out that a good swim will help his work, and then pushes him in and leaves him to drown.
Charles ELTON

A classical age-dependent Leslie matrix

Pre birth-pulse matrix:
fecundities x 1st year survival = « net fecundities »

$$M = \begin{pmatrix} f_1 s_1 & f_2 s_1 & \dots & f_i s_1 & \dots & f_n s_n \\ s_2 & 0 & \dots & 0 & \dots & 0 \\ 0 & s_3 & \dots & 0 & \dots & 0 \\ \dots & \dots & \dots & \dots & \dots & \dots \\ 0 & \dots & \dots & s_{i+1} & \dots & \dots \\ \dots & \dots & \dots & \dots & \dots & \dots \\ 0 & 0 & \dots & \dots & s_n & 0 \end{pmatrix}$$

Aging + survival:
survival probabilities
on 1st sub-diagonal

MANY age classes over ONE time step

t-1 t

N_1 $N_1 = \Sigma f_i s_1 N_i(t-1)$
N_2 $N_2 = s_2 N_1(t-1)$
N_3 $N_3 = s_3 N_2(t-1)$
...
N_{n-1} $N_{n-1} = s_{n-1} N_{n-2}(t-1)$
N_n $N_n = s_n N_{n-1}(t-1)$

MANY age classes over ONE time step

t-1 t

N_1 $N_1 = \Sigma f_i s_1 N_i(t-1)$
N_2 expands as
N_3
...
N_{n-1}
N_n

MANY age classes over ONE time step

t-1 t

N_1 $N_1 = f_1 s_1 N_1(t-1)$
N_2 $+ f_2 s_1 N_2(t-1)$
N_3 $+ f_3 s_1 N_3(t-1)$
... $+ \dots$
N_{n-1} $+ f_{n-1} s_1 N_{n-1} t-1)$
N_n $+ f_n s_1 N_n(t-1)$

ONE age class over MANY time steps

t-n	...	t-3	t-2	t-1	t
N_1	...	N_1	N_1	N_1	$N_1 = f_1\, s_1\, N_1(t-1)$ +
			N_2	N_2	$+ f_2\, s_1\, s_2\, N_1(t-2)$
				N_3	$+ f_3\, s_1\, s_2\, s_3\, N_1(t-3)$
				...	+ ....
				N_{n-1}	$+ f_{n-1} s_1 s_2 \ldots s_{n-1} N_1(t-n+1)$
				N_n	$+ f_n\ \ s_1 s_2 \ldots s_n\ \ N_1(t-n)$

Renewal equation $N_1(t) = \Sigma\, f_i\, l_i\, N_1(t-i)$ with $l_i = s_1 \ldots s_i$

Euler-Lotka equation

$N_1(t) = \Sigma\, f_i\, l_i\, N_1(t-i)$ with $l_i = s_1 \ldots s_i$

However, under asymptotic regime: $N_1(t-i) = \lambda^{-i} N_1(t)$

Hence: $N_1(t) = \Sigma\, f_i\, l_i\, \lambda^{-i} N_1(t)$

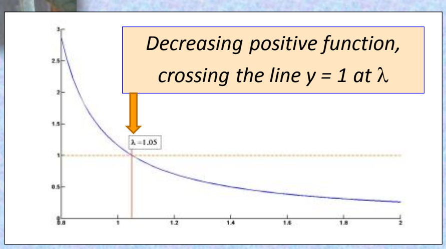
i.e. $1 = \Sigma\, f_i\, l_i\, \lambda^{-i}$

Valid for any number of age classes (even ∞)

Euler - Lotka equation
1760 and 1911, respectively

Euler-Lotka equation

Swallow example



Decreasing positive function, crossing the line y = 1 at λ

Two sides of the same coin

Stable Pop.Theory
Euler - Lotka equation
1760 and 1911, respectively

Leslie Matrices
Age-structured Matrix models
1945, 1948

Stable Population Theory to be expanded later to stage-structured matrix models

Generation time

time	t-n	...	t-3	t-2	t-1	t
contribution	$f_n\, l_n\, \lambda^{-n}$	...	$f_3\, l_3\, \lambda^{-3}$	$f_2\, l_2\, \lambda^{-2}$	$f_1\, l_1\, \lambda^{-1}$	$\Sigma = 1$
age of mothers at t	n	...	3	2	1	

Stable distribution of the Age of mothers at birth

Mean age of mothers at birth (in asymptotic regime)

$$T = \Sigma\, i\, f_i\, l_i\, \lambda^{-i}$$

$\overline{T}$, *Generation time, Leslie 1966,*
Hereafter denoted as T

Derived quantities

Number of individuals per mother in next generation

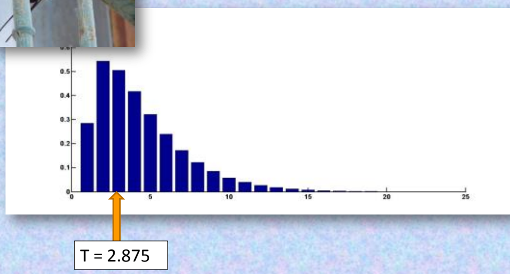
$$R_0 = \Sigma\, f_i\, l_i$$

Mean age of child birth along a mother's life

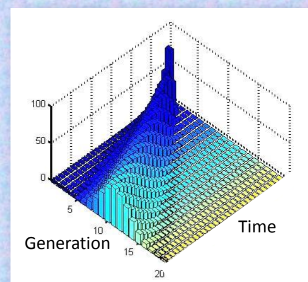
$$T_C = \Sigma\, i\, f_i\, l_i \,/\, \Sigma\, f_i\, l_i$$

Cohort Generation Time

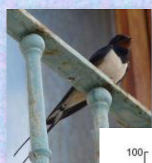
Generation time
Swallow example

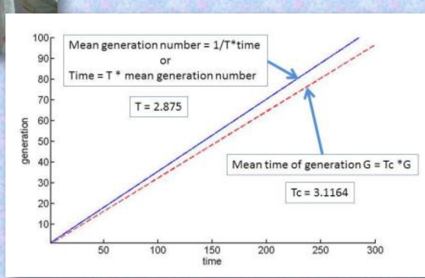


Generation waves
Swallow example



Generation waves
Swallow example





Nathan Keyfitz, 1913-2010

Generation time and Sensitivity Analysis

The Euler-Lotka equation is an implicit function, linking any generic parameter θ and λ:

$$\phi(\theta,\lambda) = \Sigma f_i(\theta) l_i(\theta) \lambda(\theta)^{-i} = 1$$

If $\theta \rightarrow \theta + d\theta$, $\lambda \rightarrow \lambda + d\lambda$, but ϕ remains equal to1, i.e. $d\phi = 0$

As a consequence $0 = \frac{\partial\phi}{\partial\lambda} d\lambda + \frac{\partial\phi}{\partial\theta} d\theta$

Hence $d\lambda/d\theta = -(\partial\phi/\partial\theta) / (\partial\phi/\partial\lambda)$

Generation time and Sensitivity Analysis

$$d\lambda/d\theta = -(\partial\phi/\partial\theta) / (\partial\phi/\partial\lambda)$$

From $\phi = \Sigma f_i l_i \lambda^{-i}$, $\partial\phi/\partial\lambda = \Sigma i f_i l_i \lambda^{-i-1} = -T/\lambda$

From $l_i = s_1 \dots s_i$, $\partial\phi/\partial s' = \Sigma f_i (l_i/s_1)\lambda^{-i} = (1/s_1)\Sigma f_i l_i \lambda^{-i} = 1/s_1$

Sensitivity $d\lambda/ds_1 = \lambda/(s_1 T)$

Elasticity $(s_1/\lambda)\, d\lambda/ds_1 = 1/T$

same result for a change in all fecundities
same result for all parameters < 1st reprod.
(« immature parameters »)

Generation time and turnover

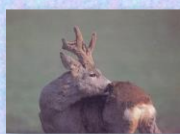
Elasticity $(s_1/\lambda)\, d\lambda/ds_1 = 1/T$

However $(s_1/\lambda)\, d\lambda/ds_1 = u_1 v_1$
under $\Sigma u_i v_i = 1$

Hence $\boxed{1/T} = u_1 v_1$ under $\Sigma u_i v_i = 1$

A measure of turnover:

- *the proportion of new individuals, in reproductive value*
- *Also the asymptotic increase in mean generation number per year*



Sensitivity analysis
Survival

$M \rightarrow M_h = (1-h)M$ $MV=\lambda V \Rightarrow (1-h)MV=(1-h)\lambda V$

Hence $M_h V = (1-h)\lambda V$

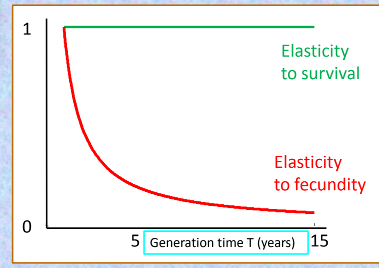
$\lambda \rightarrow \lambda_h = (1-h)\lambda$, asymptotic structure V unchanged

x % change in all s_i → x % change in λ

The elasticity of λ wrt to $\{ s_1, s_2, \ldots, s_i, \ldots\}$ is 1

Jean Clobert

Sensitivity analysis
Fecundity and Survival
Lebreton and Clobert 1991



Sensitivity analysis and Generation time

Albatross, T≈24 y:
-30 % in Fecundity $\Rightarrow$
-1.25 % in growth rate

In any sharp-decline of a long lived species, first suspect a change in survival

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